Taylor & Francis
Taylor & Francis Group

Alcheringa: An Australasian Journal of Palaeontology

ISSN: 0311-5518 (Print) 1752-0754 (Online) Journal homepage: http://www.tandfonline.com/loi/talc20

Kutjamarcoot brevirostrum gen. et sp. nov., a new short-snouted, early Miocene bandicoot (Marsupialia: Peramelemorphia) from the Kutjamarpu Local Fauna (Wipajiri Formation) in South Australia

P.M. Chamberlain, K.J. Travouillon, M. Archer & S.J. Hand

To cite this article: P.M. Chamberlain, K.J. Travouillon, M. Archer & S.J. Hand (2016) Kutjamarcoot brevirostrum gen. et sp. nov., a new short-snouted, early Miocene bandicoot (Marsupialia: Peramelemorphia) from the Kutjamarpu Local Fauna (Wipajiri Formation) in South Australia, Alcheringa: An Australasian Journal of Palaeontology, 40:2, 197-206, DOI: 10.1080/03115518.2016.1103525

To link to this article: http://dx.doi.org/10.1080/03115518.2016.1103525

Kutjamarcoot brevirostrum gen. et sp. nov., a new short-snouted, early Miocene bandicoot (Marsupialia: Peramelemorphia) from the Kutjamarpu Local Fauna (Wipajiri Formation) in South Australia

P.M. CHAMBERLAIN, K.J. TRAVOUILLON, M. ARCHER and S.J. HAND

Chamberlain, P.M., Travouillon, K.J., Archer, M. & Hand, S.J., November 2015. *Kutjamarcoot brevirostrum* gen. et sp. nov., a new short-snouted, early Miocene bandicoot (Marsupialia: Peramelemorphia) from the Kutjamarpu Local Fauna (Wipajiri Formation) in South Australia. *Alcheringa 40*, 197–206. ISSN 0311-5518.

A new bandicoot species, *Kutjamarcoot brevirostrum* gen. et sp. nov. (Peramelemorphia), is described here from the Leaf Locality, Kutjamarpu Local Fauna (LF), Wipajiri Formation (South Australia). The age of the fossil deposit is interpreted as early Miocene on the basis of biocorrelation between multiple species in the Kutjamarpu LF and local faunas from the Riversleigh World Heritage Area (WHA). *Kutjamarcoot brevirostrum* is represented by isolated teeth and three partial dentaries and appears to have been short-snouted with an estimated mass of 920 g. Phylogenetic analyses place *K. brevirostrum* in a clade with extant Australian bandicoots and the extinct *Madju*, but potentially exclude the extant New Guinean bandicoots. Morphometric analysis infers close similarity between *K. brevirostrum* and species of *Galadi* in both size and rostral length. They, thus, potentially occupied compatible ecological niches with competitive exclusion perhaps explaining geographical segregation between these broadly coeval lineages.

Philippa M. Chamberlain [philippa.chamberlain@uq.net.au], School of Earth Sciences, University of Queensland, St Lucia, Queensland 4072, Australia; Kenny J. Travouillon [kenny.travouillon@museum.wa.gov.au; kennytravouillon@hotmail.com], Western Australian Museum, Locked Bag 49, Welshpool DC, WA, 6986, and School of Earth Sciences, University of Queensland, St Lucia, Queensland, 4072, Australia; Michael Archer [m.archer@unsw.edu.au] and Suzanne J. Hand [s.hand@unsw.edu.au], School of Biological, Earth and Environmental Sciences, University of New South Wales, New South Wales, 2052, Australia. *Received 15.4.2015; revised 29.9.2015; accepted 1.10.2015.*

Key words: Peramelemorphia, phylogeny, *Kutjamarcoot brevirostrum*, Kutjamarpu Local Fauna.

BANDICOOTS, members of the Order Peramelemorphia, are small, omnivorous marsupials endemic to Australia, New Guinea and surrounding islands (Armati *et al*. 2006). Currently, four families of peramelemorphians are recognized: Peramelidae (true bandicoots), Thylacomyidae (bilbies), Chaeropodidae (pig-footed bandicoots) and Yaralidae, an extinct Oligocene/Miocene group. Several fossil genera, including *Galadi*, *Bulungu* and *Madju*, remain without family classification (Westerman *et al*. 2012, Travouillon *et al*. 2014a).

Although the Riversleigh World Heritage Area (WHA) in northwestern Queensland has been highly productive in terms of revealing many new Oligocene and Miocene peramelemorphians (Muirhead & Filan 1995, Muirhead 2000, Travouillon *et al*. 2010, 2013a, b, 2014a, b, Gurovich *et al*. 2014), several Miocene species have also been recovered from the Kutjamarpu Local Fauna (LF) at the Leaf Locality in the Wipajiri Formation of northern South Australia. The Miocene Wipajiri Formation represents the sedimentary fill of a fluviatile channel cut unconformably into the top of the underlying late Oligocene Etadunna Formation (Woodburne *et al*. 1993). The Kutjamarpu LF is interpreted to be of early Miocene age based on biocorrelation with deposits from the Riversleigh WHA (Archer *et al*. 1997, Travouillon *et al*. 2006, Megirian *et al*. 2010). Taxa shared by the Kutjamarpu LF and early Miocene LFs at Riversleigh include: *Emuarius gidju, Litokoala kutjamarpensis*, *Rhizophascolonus crowcrofti, Wakaleo oldfieldi, Ektopodon serratus, Paljara tirarensae, Marlu kutjamarpensis, M. ampelos, M. syke, Bulungu palara, Madju variae* and *Wakiewakie lawsoni* (Travouillon *et al*. 2014a, b). Some of these taxa also extend into the middle Miocene at Riversleigh. The previously estimated ages of the Riversleigh LFs have now been corroborated by radiometric dates (Woodhead *et al*. in press). The present study describes a new peramelemorphian from the Kutjamarpu LF.

Materials and methods

All specimens were collected from the Wipajiri Formation, at the Leaf Locality, of South Australia by

http://dx.doi.org/10.1080/03115518.2016.1103525

screen-washing matrix in the field (Campbell 1976). The specimens are registered with the University of California, Museum of Paleontology and the South Australian Museum, Adelaide (SAM P). Dental terminology follows Archer (1976), Muirhead & Filan (1995), Voss & Jansa (2003) and Travouillon *et al.* (2010).

Specimens were photographed and measured using a Leica camera DFC450C attached to a Leica binocular microscope M80, and the software program LAS v4.3. Images obtained were edited using Photoshop CS5. Some of the specimens, which had previously been coated with gold for SEM photography, were coated in magnesium oxide to minimize light reflection.

Phylogenetic Analysis

The phylogenetic relationships of *Kutjamarcoot brevirostrum* gen. et sp. nov. were investigated using the character set and matrix from Travouillon *et al.* (2014a). The matrix is composed of 123 dental and 33 cranial morphological characters. The morphology of *K. brevirostrum* was scored and added to the matrix, resulting in the analysis of 47 taxa. Following Travouillon *et al.* (2014a), *Djarthia murgonensis* [the oldest australidelphian marsupial (Beck 2008)], *Barinya wangala* [the oldest dasyuromorphian (Wroe 1999)], *Mutpuracinus archibaldi* [thylacinid (Murray & Megirian 2000)], and *Dasyurus hallucatus*, *Dasyuroides byrnei*, *Phascogale tapoatafa*, *Antechinus stuartii* and *Sminthopsis macroura* (dasyuromorphians) were used as outgroups.

Two parsimony analyses of the matrix were undertaken. Following Travouillon *et al.* (2014a), the first analysis was unconstrained, whereas the second analysis was constrained, using a 'molecular scaffold' based on the molecular phylogeny of Westerman *et al.* (2012). These analyses were conducted using PAUP* 4.0b10 (Swofford 2002). Each parsimony analysis was conducted in two stages: an initial heuristic search comprising 1000 replicates, retaining eight trees per replicate; and then a second heuristic search conducted using the saved trees from the initial search. A strict consensus was used to summarize the most parsimonious trees. Following this, bootstrap values for each node were calculated using 1000 bootstrap replicates consisting of 10 random addition sequence replicates and decay indices calculated using TreeRot 3.0 (Sorenson & Franzosa 2007).

Morphometric Analysis

Principal-component analysis (PCA) of the upper and lower dental measurements was performed using the

	P3		M1		M2		M3	
Specimen	**L**	**W**	**L**	**W**	**L**	**W**	**L**	**W**
SAMP17917							2.93	2.716
SAMP50825							3.272	3.166
SAMP50826					3.077	3.186		
SAMP50831			3.098	2.669				
SAMP50832	2.55	1.796						
UCMP102442			2.922	2.211				

Table 1. Measurements of the upper dentition of type and referred material of *Kutjamarcoot brevirostrum* in millimetres. L = anteroposterior length; W = lingual-buccal width; P = premolar; M = molar.

	m1			m2			m3			m4		
Specimen	**L**	**AW**	**PW**	**L**	**AW**	**PW**	**L**	**AW**	**PW**	**L**	**AW**	**PW**
SAMP50824	2.914	1.656	2.033									
SAMP50829	2.672	1.608	2.006									
SAMP50830							2.773	1.66	1.872			
SAMP50833					1.754	1.961						
UCMP100275				2.781	1.659	1.975	2.953	1.869	2.062	2.835	1.518	1.132
UCMP100277					1.321	1.697						
UCMP100280				2.968	1.717	2.023	2.944	1.866	2.066			
UCMP100281				2.987	1.687	1.787						
UCMP100282							2.751	1.866	2.034			
UCMP107799							3.239	1.828	1.913			
UCMP108071				2.93	1.652	2.107						
UCMP108073				3.05	1.631	1.901						
UCMP66842	2.656	1.505	1.755									
UCMP66843					1.959	2.148						

Table 2. Measurements of the lower dentition of type and referred material of *Kutjamarcoot brevirostrum* in millimetres. L = anteroposterior length; AW = anterior width; PW = posterior width; p = premolar; m = molar.

program PAST, version 2.17c (Hammer *et al*. 2001). Dental measurements of specimens of *Kutjamarcoot brevirostrum* were compared with similar-aged specimens from Riversleigh (WHA), including: *Bulungu palara* (Gurovich *et al*. 2014), Riversleigh genus 3 sp. 1 (Archer *et al*. 2006), Riversleigh genus 5 spp. 1 and 2 (Archer *et al*. 2006), *Yarala burchfieldi* (Muirhead & Filan 1995), *Galadi speciosus* (Travouillon *et al*. 2010), *G. amplus, G. grandis, G. adversus* (Travouillon *et al*. 2013a), *Madju variae* and *M. encorensis* (Travouillon *et al*. 2014b). Dental measurements were compiled for *K. brevirostrum* (Tables 1 and 2) and the other comparative species listed above (supplementary data).

Body Mass Estimate

The body mass of *Kutjamarcoot brevirostrum* was estimated using Myers' (2001) allometric relationships between dental measurements and marsupial body mass. The highest ranked equation was selected to estimate body mass from the dataset 'all species excluding dasyuromorphians' (Myers 2001). The chosen equation was for the lower third molar length (3LML). Measurements were averaged to accommodate for multiple specimens.

Systematic palaeontology

Order PERAMELEMORPHIA (Kirsch, 1968) Aplin & Archer, 1987
Superfamily PERAMELOIDEA (Waterhouse, 1838)
Family INCERTAE SEDIS

Kutjamarcoot gen. nov.

Kutjamarcoot brevirostrum sp. nov. (Figs 1–3)

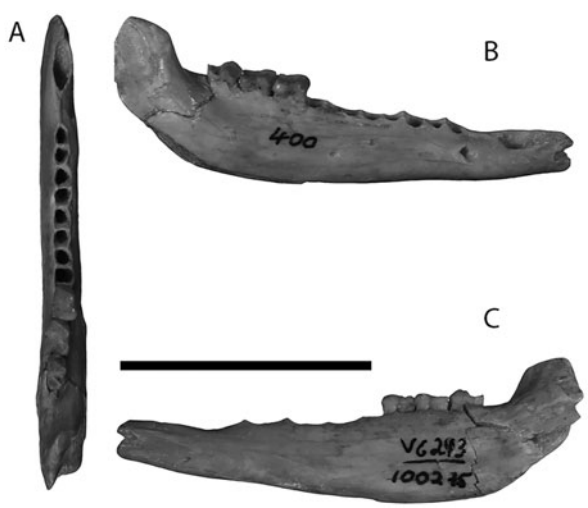

Fig. 1. Holotype of *Kutjamarcoot brevirostrum* gen. et sp. nov., UCMP100275, right dentary with m2–4. **A**, Occlusal view; **B**, Buccal view; **C**, Lingual view. Scale bar = 20 mm.

Generic and specific differential diagnosis

Kutjamarcoot brevirostrum differs from chaeropodids in having an anterior cingulum on all upper molars, a preparacrista that connects to StB on M1, and a cristid obliqua that terminates between the protoconid and the midpoint of the metacristid on m1–3. It differs from thylacomyids in having a metaconule on all upper molars. It differs from peramelids and the species *Crash bandicoot* in lacking a posterior cingulum on M1. It differs from echypimerines and peroryctines in having the paraconid/metaconid distance shorter than the length of the metacristid on m2–m4. It differs from other Oligo–Miocene taxa, such as species of *Yarala*, *Galadi* and *Bulungu*, in having no contact between the premetacrista and postparacrista on all upper molars, and having no StE on any upper molars. It differs from species of *Madju* in having no diastema between p1 and p2, shorter lower molars, shorter and wider P3, better developed metaconule on all upper molars, and no StE on any of the upper molars. *Kutjamarcoot brevirostrum* differs from all peramelemophian taxa in having a StD1 on M3.

Etymology. Kutjamarcoot is a combination of Kutjamarpu (location where the genus/species was found) and bandicoot. *Brevirostrum* is a Latin word (gender neuter) meaning short nose, in reference to the short snout of this species.

Holotype. UCMP100275, right dentary with m2–4 and alveoli for c1, p1–3 and m1.

Paratypes. SAM P50824, isolated right m1; UCMP100281, partial right dentary with m2; UCMP100282, isolated left m3; SAM P50832, isolated right P3; UCMP102442, isolated left M1; SAM P50826, isolated left M2; SAM P50827, broken isolated left M2 (missing most of metastylar shelf); SAM P17917, isolated left M3.

Referred material. UCMP100280, left dentary with m2–3; UCMP66842, isolated right m1; SAM P50833, broken isolated right mx (breakage at hypoconulid and postparaconid); SAM P50829, isolated left m1; UCMP108071, isolated right m2; UCMP108073, broken isolated left m2 (cracked on talonid); UCMP107799, isolated right m3; SAM P50830, isolated left m3; UCMP100277, broken isolated right mx (most of trigonid missing); UCMP66843, broken isolated left mx (most of talonid missing), SAM P50831, isolated right M1; SAM P50825, isolated left M3; SAM P50828, isolated left broken M1; UCMP66832, broken right M2; UCMP108070, broken right M3.

Type locality. All type and referred specimens are from the Leaf Locality, site code V6213 (University of

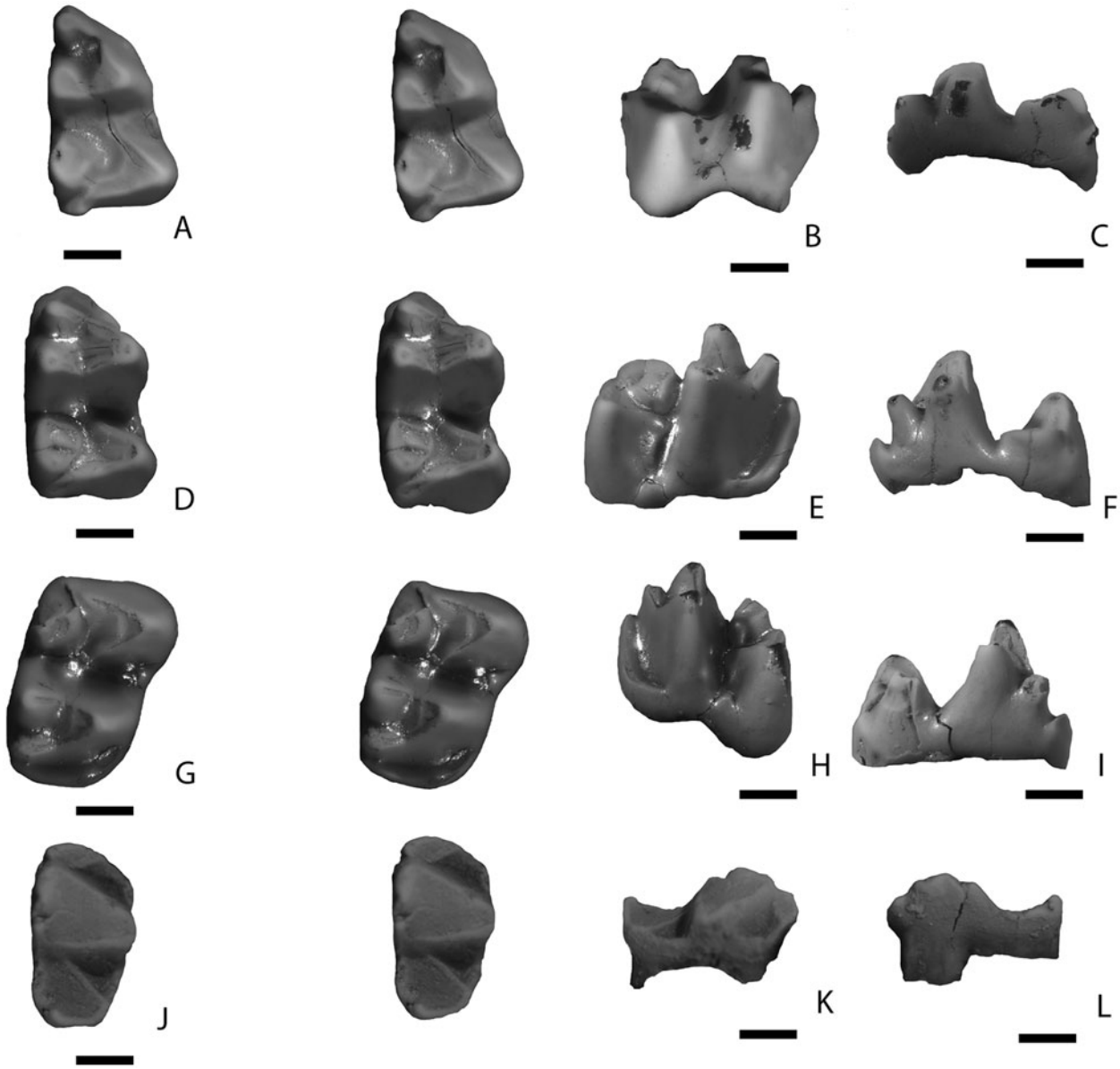

Fig. 2. Lower dentition of *Kutjamarcoot brevirostrum* gen. et sp. nov. Paratype SAM P50824, right m1; **A**, Occlusal view stereo pair; **B**, Buccal view; **C**, Lingual view. Paratype UCMP100281, right m2; **D**, Occlusal view stereo pair; **E**, Buccal view; **F**, Lingual view. Paratype UCMP100282, left m3; **G**, Occlusal view stereo pair; **H**, Buccal view; **I**, Lingual view. Holotype UCMP100275, right m4; **J**, Occlusal view stereo pair; **K**, Buccal view; **L**, Lingual view. Scale bar = 2 mm.

California Site catalogue), east side of Lake Ngapakaldi, Tirari Desert, South Australia

Age and stratigraphy. The Leaf Locality, which has produced the Kutjamarpu LF, occurs within the Wipajiri Formation, which is estimated to be early Miocene in age (Archer *et al*. 1997, Travouillon *et al*. 2006).

Description

Dentary. The holotype is a right dentary (Fig. 1) and, being in best condition, is the basis of this description. Other specimens are not seen to differ significantly in their morphology. The dentary is deepest below m3. In lateral view, the dorsal margin of the ramus is mostly rectilinear, whereas the ventral margin is convex. Only m2–4 are preserved in the holotype, but alveoli for c1, p1–3 and m1 are preserved. There is a short diastema between c1 and p1. No other diastemata are present. The lengths of the alveoli indicate that the premolars increase in length posteriorly. Two mental foramina are present on the buccal side of the dentary, the larger of the two below the anterior root of p1, and the smaller below the posterior root of m1. The anterior margin of the ascending ramus forms a 120° angle with the alveolar plane of the horizontal ramus. The symphysis is relatively smooth and extends posteriorly to a point level with the anterior end of p2.

Lower dentition. No anterior cingulum is present on m1, although a cingulum-like bulge is present on the

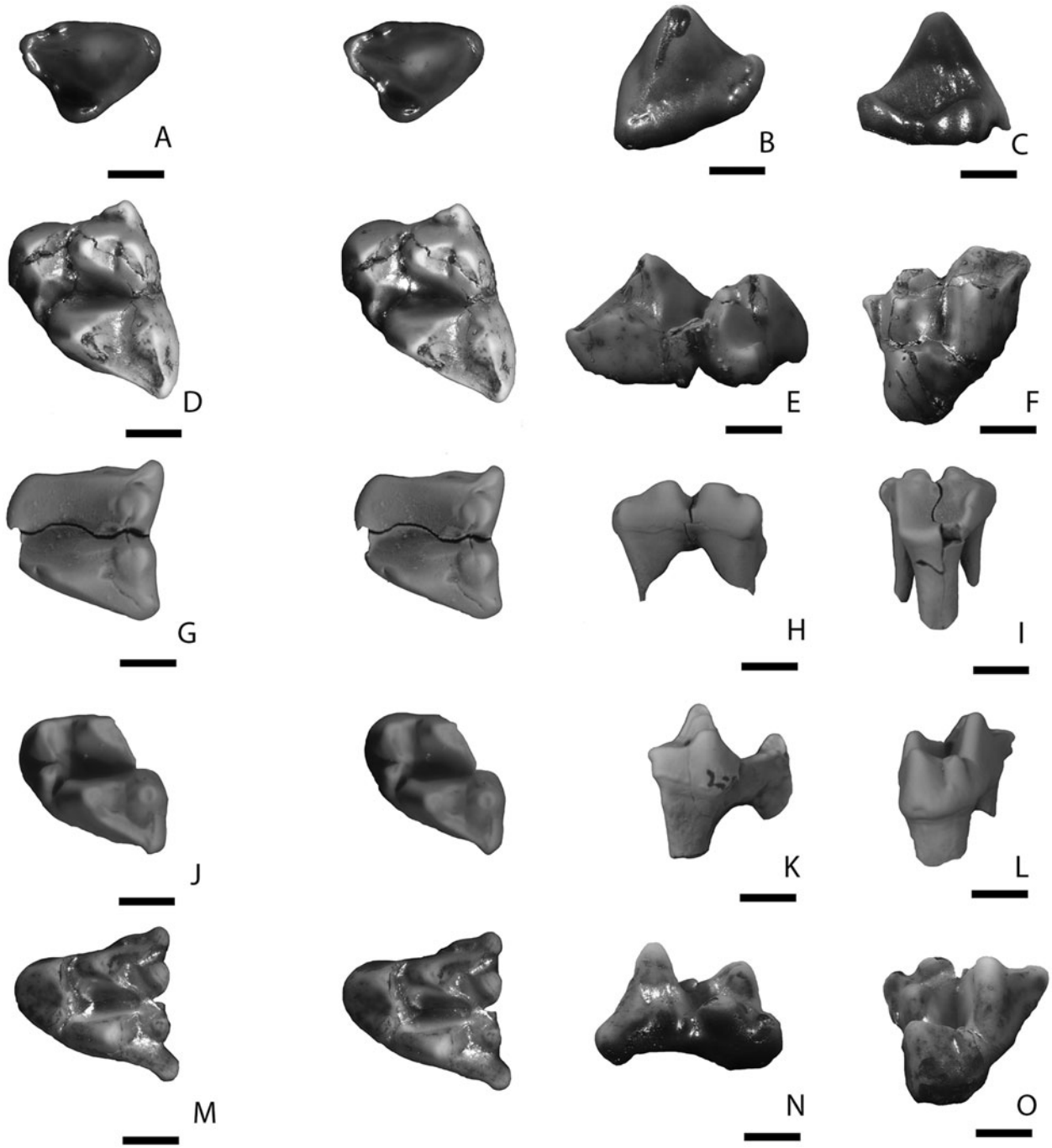

Fig. 3. Upper dentition of *Kutjamarcoot brevirostrum* gen. et sp. nov. Paratype SAM P50832, right P3; **A**, Occlusal view stereo pair; **B**, Buccal view; **C**, Lingual view; paratype UCMP102442, left M1; **D**, Occlusal view stereo pair; **E**, Buccal view; **F**, Lingual view; paratype SAM P50826, left M2; **G**, Occlusal view stereo pair; **H**, Buccal view; **I**, Lingual view; paratype SAM P50827, left M2; **J**, Occlusal view stereo pair; **K**, Buccal view; **L**, Lingual view; paratype SAM P17917, left M3; **M**, Occlusal view stereo pair; **N**, Buccal view; **O**, Lingual view. Scale bar = 2 mm.

antero-basal surface of the paraconid (Fig. 2A–C). The talonid is longer and wider than the trigonid. The distance between the paraconid and metaconid is the same as the length of the metacristid. The paracristid is longer than the metacristid. The paraconid is directly anterior to the metaconid. A pre-entocristid is present anteriorly on the anterior flank of the entoconid. The posthypocristid is oblique to the tooth row axis and connects to a large hypoconulid. The cristid obliqua terminates on the back of the trigonid at a point almost midway across the posterior flank of the metacristid.

The morphology of m2 (Fig. 2D–F) is like that of m1, except as follows. A moderate-sized anterior cingulum is present. The trigonid is shorter but wider than the trigonid on m1. The paraconid/metaconid distance is much shorter than it is in m1 and the paracristid and metacristid are equidistant. The entoconid is more prominent, being wider and more rounded than that of

m1. The cristid obliqua terminates more lingually, exactly level with the midpoint of the metacristid. The hypoconid is positioned more anteriorly.

The m3 (Fig. 2G–I) is similar to m2 except as follows. The anterior cingulum is longer. The hypoconulid is reduced. The talonid is wider.

The m4 (Fig. 2J–L) is similar to m3 except as follows. The anterior cingulum is longer. The posthypocristid is perpendicular to the tooth row. The cristid obliqua terminates more lingually. The talonid is greatly reduced in size.

Upper dentition. The P3 is triangular in occlusal view (Fig. 3A). The main cusp is located centrally and enlarged laterally (Fig. 3A–C). The weakly developed lingual cingulum has a very small lingual cusp. The anterior cusp is small, with no anterior crest joining it to the main cusp. The posterior cusp, which is the smallest of all cusps on the P3, is joined to the main cusp by a posterior crest.

The M1 (Fig. 3D–F) has a short anterior cingulum extending lingually from StA to a point about half way to the paracone. It does not connect to the preprotocrista. The buccal side of the tooth is straight. The preparacrista departs from the paracone anterobucally and ends at the anterolingual flank of StB. StB and StC are fused yet distinguishable in buccal view. They form a larger lacriform cusp with St B larger than St C. St B/St C do not connect to StD. A small StD1 is present just anterior of StD. StD is the highest cusp on M1. A crest connects StD to the metastyle, with no distinct StE present. The premetacrista does not join to the postparacrista, a feature that is similar to modern bandicoots (Long 2002, Travouillon *et al*. 2014a, b). This creates a distinct valley dividing the metastylar and parastylar shelves. The metacone lies directly lingual to StD. The metaconule is small and anterolingually positioned relative to the metacone, with a small shelf present between the base of the metacone and the metaconule. No posterior cingulum is present. The metaconule is joined to the protocone by the postprotocrista, which itself is concave, bending back towards the tooth interior. The protocone lies lingual to the paracone. The preprotocrista is straight and continues from the protocone, ending at the anterior flank of the paracone.

M2 (Fig. 3G–L) is similar to M1 except as follows. It is much wider, increasing the lengths of all crests. The anterior cingulum is wider also. The paracone is extended lingually. StA is larger and taller and is on the parastylar shelf. The preparacrista joins StA to the paracone. StB is more rounded and more circular in cross-section. There is no StC. StD is shorter with no connection to the crest running to the metastyle. The metaconule is larger. The distance between the metaconule and protocone is increased, which lengthens the postprotocrista.

M3 (Fig. 3M–O) is similar to M2 except as follows. The tooth is wider, extending the lengths of all crests. The ectoloph is more distinct. A small StD1 is present anterior to StD. The metaconule is smaller and positioned more anteriorly. The metastyle is positioned more buccally, with stylar crest running anteriorly.

Results

Phylogenetic analysis

The results of the phylogenetic analysis are summarized as two strict consensus trees based on maximum parsimony analysis of a 156 character craniodental matrix (Fig. 4). The first consensus tree (Fig. 4A) was processed without the 'molecular scaffold'. It shows that the initial division between superfamilies Yaraloidea and Perameloidea is robustly supported (bootstrap value = 99, decay index = 9), as is monophyly of species of *Yarala* (bootstrap = 97%) and *Galadi* (bootstrap = 56%). A clade containing *Bulungu* (*B. palara, B. muirheadae* and *B. campbelli*) and cf. *Peroryctes* (*Peroryctes* sp and *P. tedfordi*) is then recovered as sister group to all remaining perameloids (bootstrap <50%). Peramelidae is not recovered as a monophyletic clade, with Peramelinae forming a clade with Thylacomyidae and Chaeropodidae, though support values are low (bootstrap <50%). Echymiperinae and Peroryctinae are recovered as paraphyletic groups, but with low bootstrap values (bootstrap <50%). The phylogenetic position of *Kutjamarcoot brevirostrum* remains unresolved with species of *Madju,* as sister taxa to Peramelinae, Thylacomyidae and Chaeropodidae (bootstrap >50%) The monophyly of *Isoodon* is recovered with strong support (bootstrap = 96%). Species of *Madju* are monophyletic with some support (bootstrap = 63%). Moreover, separation of this clade from two other weakly defined clades, the first containing *Bulungu* and cf. *Peroryctes* and the second containing *Peroryctinae* and *Echymiperinae*, is also only weakly supported (bootstrap <50%).

Although the second tree (Fig. 4B) is constrained by a 'molecular scaffold', the tree is less resolved. Although high bootstrap values again define Perameloidea and Yaraloidea, many weaker branches from the first tree have been lost. Although *K. brevirostrum* is still within the superfamily Perameloidea (bootstrap = 61%), it is one branch in an unresolved polytomy within that superfamily.

PCA

For PCA of the upper dentition (Fig. 5A), Component 1 accounts for 66.36% of the variance and Component 2 for 12.72% of the variance. Other components account for less than 8% (e.g., Component 3 = 6.52%). The length and width of M2 and M3 were the most

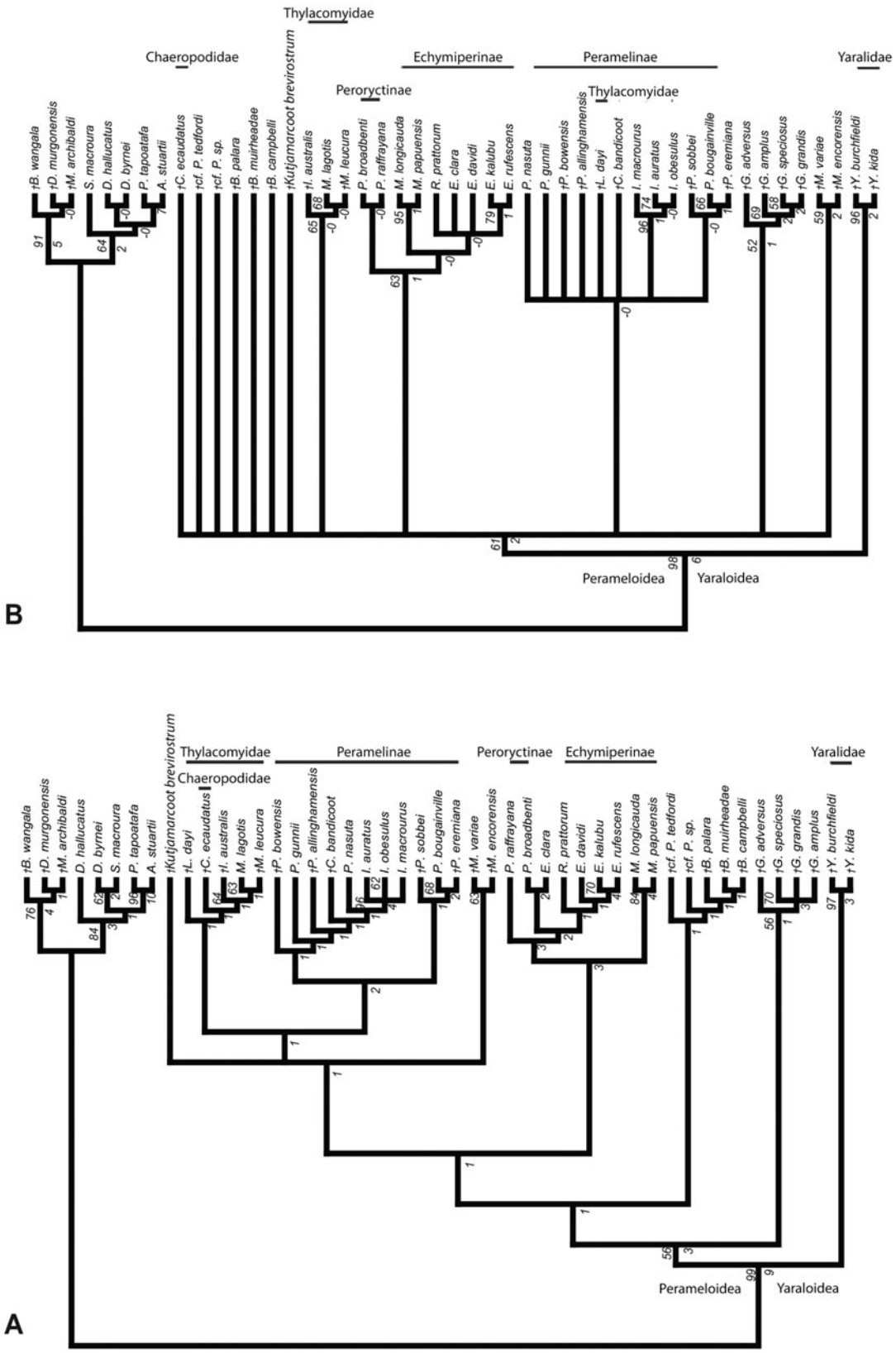

Fig. 4. Parsimony analysis of *Kutjamarcoot brevirostrum* gen. et sp. nov. **A**, Unconstrained consensus tree (tree length = 879, consistency index excluding uninformative characters (CI) = 0.2912 and retention index (RI) = 0.6496); **B**, Constrained consensus tree using a 'molecular scaffold' (tree length = 825, CI = 0.3057 and RI = 0.6182). †Fossil and recently extinct taxa. Numbers above (to the left of) branches represent bootstrap values (1000 replicates), whereas numbers below (to the right of) branches represent decay indices.

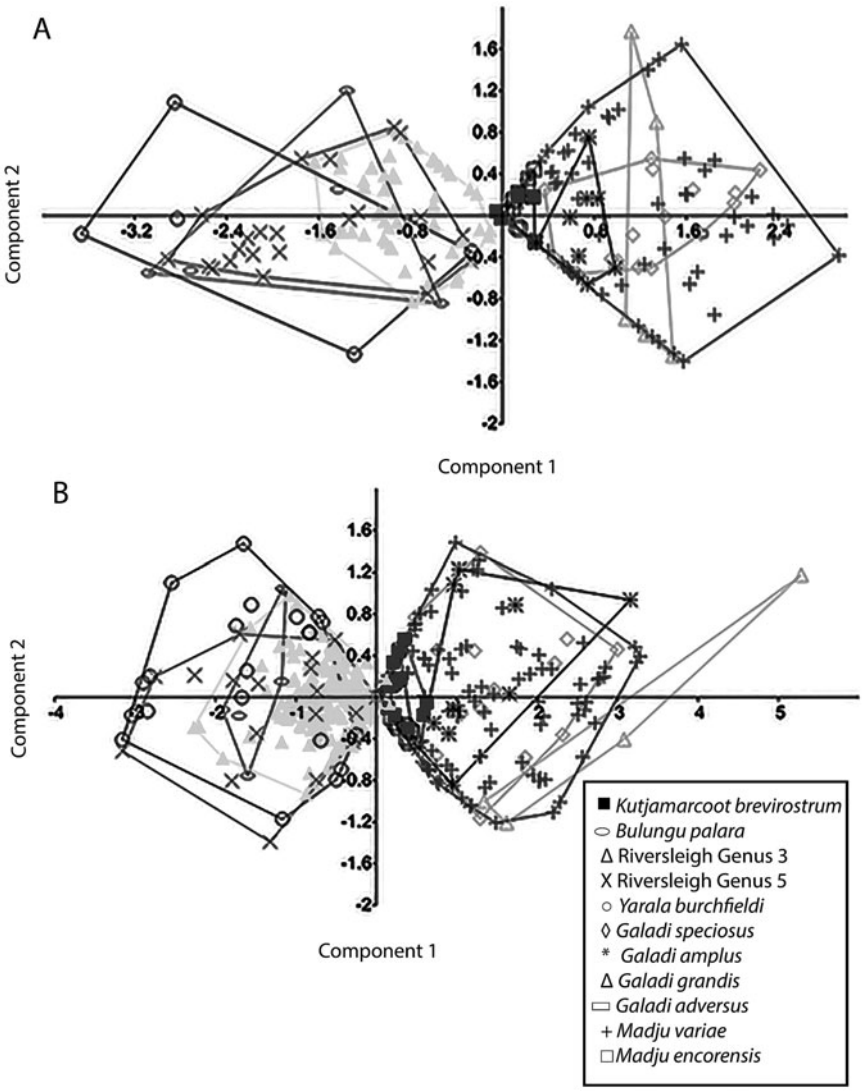

Fig. 5. Principal-component analysis with convex hulls of log transformed **A**, upper and **B**, lower dentition measurements of the Kutjamarpu LF and Riversleigh WHA fossil species.

informative for separating species along Component 1. *Kutjamarcoot brevirostrum* results overlap with the results for *Madju variae* and *M. encorensis*. It is also closely bordered by *Galadi amplus* and *G. speciosus*.

For PCA of the lower dentition (Fig. 5B), Component 1 accounts for 66.91% of the variance and Component 2 for 10.44% of the variance (other components account for <8% each, with Component 3 = 7.40%). The lengths of the molars were most informative for distinguishing species along Component 1. Similarly to the upper dentition results, *K. brevirostrum* overlaps with *M. variae*, and *M.* encorensis and *G. speciosus*. *Kutjamarcoot brevirostrum* is again bordered by *G. amplus*.

Body mass estimate

The body mass for *Kutjamarcoot brevirostrum*, using measurements from five m3s, is estimated to have been 920 g (Table 3).

Specimen	Molar length (mm)	Estimated mass (g)
UCMP107799	3.239	961.2
UCMP100282	2.751	909.0
SAMP50830	2.773	911.5
UCMP100275	2.953	931.3
UCMP100280	2.944	930.4
Average	2.932	920.8

Table 3. Estimated mass (g) based on measurements of the third lower molar.

Discussion

The lack of diastemata between any premolars on the dentary (Fig. 1) suggests that *Kutjamarcoot brevirostrum* was short-snouted. Among living bandicoots, only species of *Isoodon* are classified as being short-snouted (Van Dyke & Strahan 2008), but an analysis of the snout length and width of a range of peramelemorphians (Travouillon *et al*. 2010) has demonstrated that

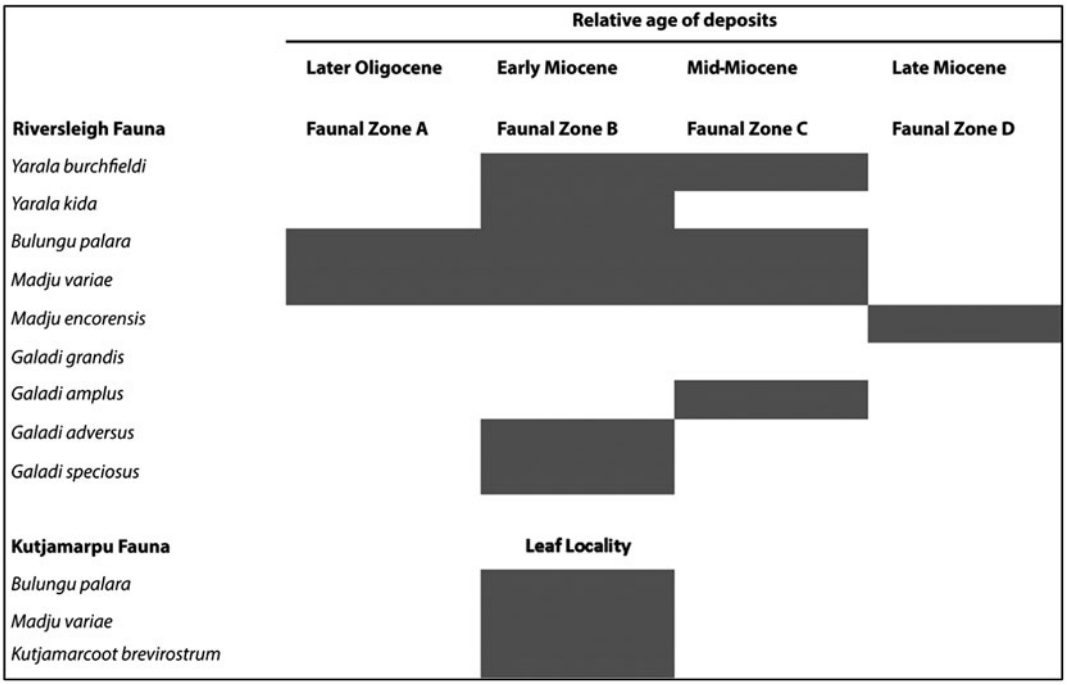

Fig. 6. Temporal occurrence of peramelemorphian species at the Riversleigh WHA and Kutjamarpu LF.

species of *Chaeropus, Macrotis, Galadi* and *Echymipera clara* also have relatively short snouts. Although species of *Galadi* are interpreted to have been more faunivorous than their more omnivorous modern relatives, it is the width of the snout that distinguishes them and suggests they could tackle relatively larger prey species (Travouillon *et al*. 2010). Without a skull for *K. brevirostrum*, it is difficult to determine its diet with the same level of confidence. However, the fact that it has a weakly developed metaconule suggests that it was probably more insectivorous than omnivorous (Muirhead & Filan 1995).

Kutjamarcoot brevirostrum is the third peramelemorphian species to be recovered from the Kutjamarpu LF, the other two being *Bulungu palara* and *Madju variae*. *Bulungu palara* is short-snouted, but very small, being close in size to modern species of *Antechinus* (Gurovich *et al*. 2014). *Madju variae* is much larger, long-snouted and similar in size and shape to *Perameles nasuta* (Travouillon *et al*. 2014b). Both *B. palara* and *M. variae* occur in Miocene deposits of the Riversleigh WHA (Fig. 6). Although *K. brevirostrum* does not occur in any of the Riversleigh Local Faunas, the similar-sized, short-snouted peramelemorphians *Galadi speciosus* does. *Galadi speciosus* has an estimated body mass of approximately 929 g (Travouillon *et al*. 2010, 2013a), similar to *Kutjamarcoot brevirostrum* (920 g). Our PCA analysis of dental measurements also implies similar dental dimensions. Therefore, we suggest that these taxa might have occupied overlapping ecological niches and, hence, potentially competed, perhaps explaining the apparent absence of *K. brevirostrum* at Riversleigh.

The phylogenetic placement of *Kutjamarcoot brevirostrum* remains highly unresolved. It can be placed confidently in the superfamily Perameloidea, as supported by both analyses, but its affinities within Perameloidea are less certain, with potentially species of *Madju* being its closest relatives. The lack of a complete centrocrista on any upper molars, found also in *Madju* and *Crash*, suggests that *K. brevirostrum* is more closely related to modern bandicoots than *Yarala, Galadi* and *Bulungu*, found in this and similar-aged deposits (Travouillon *et al*. 2014a, b). However, it is apparent that the phylogenetic results recovered here are heavily influenced by convergent morphological characters. The three molecularly robust families, Chaeropodidae, Thylacomyidae and Peramelidae (Westerman *et al*. 2012) are not recovered in this morphological matrix, probably owing to convergent dental and cranial characters between *Chaeropus, Macrotis* and *Isoodon* (e.g., large bullae, high crowned molars with enamel covered roots). This issue may be resolved with postcranial characters added to the matrix, as previously suggested (Travouillon *et al*. 2013b, 2014a, b).

Acknowledgements

We thank the University of California, Berkeley, and in particular B. Clemens, for permission to examine the University of California material. We thank C. Campbell for permission to further examine some of the peramelemorphian specimens he researched for his PhD. And we thank M. Woodburne, Clemens and Campbell for enabling one of us (MA) to participate in their 1971 expedition to the Leaf Locality, which resulted in collection of many of the specimens examined in this study.

We thank R. Day for providing funding to the University of Queensland to create a postdoctoral position for K.J. Travouillon. Support for the collection of peramelemorphians from the Riversleigh World Heritage fossil deposits has come from the Australian Research Council (LP0989969, LP100200486, DP1094569 & DP130100197 grants to M. Archer and S.J. Hand at the University of New South Wales); XSTRATA Community Partnership Program (North Queensland); the University of New South Wales; P. Creaser and the CREATE Fund; the Queensland Parks and Wildlife Service; Environment Australia; the Queensland Museum; the Riversleigh Society Inc.; Outback at Isa; Mount Isa City Council; private supporters including K. & M. Pettit, E. Clark, M. Beavis and M. Dickson; and the Waanyi people of northwestern Queensland.

References

Aplin, K.P. & Archer, M., 1987. Recent advances in marsupial systematics with a new syncretic classification. *Possums and Opossums: Studies in Evolution 1*, 15–72.

Archer, M., 1976. The dasyurid dentition and its relationships to that of didelphids, thylacinids and borhyaenids. *Australian Journal of Zoology, Supplementary Series 39*, 1–34.

Archer, M., Hand, S., Godthelp, H. & Creaser, P., 1997. Correlation of the Cainozoic sediments of the Riversleigh World Heritage fossil property, Queensland, Australia. *Mémoires et travaux de l'Institut de Montpellier 21*, 131–152.

Archer, M., Arena, D. A., Bassarova, M., BECK, R. M., Black, K., Boles, W. E., … & Wroe, S., 2006. Current status of species-level representation in faunas from selected fossil localities in the Riversleigh World Heritage Area, northwestern Queensland. *Alcheringa: An Australasian Journal of Palaeontology*, 30, 1–17.

Armati, P., Dickman, C. & Hume, I., 2006. *Marsupials*. Cambridge University Press, Cambridge, 373 pp.

Beck, R., 2008. A dated phylogeny of marsupials using a molecular supermatrix and multiple fossil constraints. *Journal of Mammalogy 891*, 175–189.

Campbell, C.R., 1976. *Tertiary Dasyuridae and Peramelidae (Marsupialia) from the Tirari Desert, South Australia*. PhD Thesis, University of California, Berkeley, 224 pp. (unpublished)

Gurovich, Y., Travouillon, K., Beck, R., Muirhead, J. & Archer, M., 2014. Biogeographical implications of a new mouse-sized fossil bandicoot (Marsupialia: Peramelemorphia) occupying a dasyurid-like ecological niche across Australia. *Journal of Systematic Palaeontology 12*, 265–290.

Hammer, Ø., Harper, D.A.T. & Ryan, P.D., 2001. PAST: Palaeontological statistics software package for education and data analysis. *Palaeontologia Electronica 4.1.4*, 1–9.

Kirsch, J.A.W., 1968. Prodromus of the comparative serology of Marsupialia. *Nature 217*, 418–420.

Long, J., 2002. *Prehistoric Mammals of Australia and New Guinea: One Hundred Million Years of Evolution*. JHU Press, Maryland, 240 pp.

Megirian, D., Prideaux, G., Murray, P. & Smit, N., 2010. An Australian land mammal age biochronological scheme. *Paleobiology 36*, 658–671.

Muirhead, J., 2000. Yaraloidea (Marsupialia, Peramelemorphia), a new superfamily of marsupial and a description and analysis of the cranium of the Miocene *Yarala burchfieldi*. *Journal of Paleontology 74*, 512–523.

Muirhead, J. & Filan, S.L., 1995. *Yarala burchfieldi*, a plesiomorphic bandicoot (Marsupialia, Peramelemorphia) from Oligo-Miocene deposits of Riversleigh, northwestern Queensland. *Journal of Paleontology 69*, 127–134.

Murray, P. & Megirian, D., 2000. Two new genera and three new species of Thylacinidae (Marsupialia) from the Miocene of the Northern Territory, Australia. *The Beagle 16*, 145–162.

Myers, T., 2001. Prediction of marsupial body mass. *Australian Journal of Zoology 49*, 99–118.

Sorenson, M. & Franzosa, E., 2007. *Treerot ver. 3.0*. Department of Biology BU, Boston, MA.

Swofford, D., 2002. *PAUP*. Phylogenetic Analysis Using Parsimony (*and Other Methods). Version 4 (Updated to 10 Beta)*. Sinauer Associates, Sunderland, Massachussets.

Travouillon, K.J., Archer, M., Hand, S.J. & Godthelp, H., 2006. Multivariate analyses of Cenozoic mammalian faunas from Riversleigh, north-western Queensland. *Alcheringa, Special Issue 1*, 323–349.

Travouillon, K.J., Gurovich, Y., Beck, R. & Muirhead, J., 2010. An exceptionally well-preserved short-snouted bandicoot (Marsupialia; Peramelemorphia) from Riversleigh Oligo-Miocene deposits, northwestern Queensland, Australia. *Journal of Vertebrate Paleontology 30*, 1528–1546.

Travouillon, K.J., Gurovich, Y., Archer, M., Hand, S.J. & Muirhead, J., 2013a. The genus *Galadi:* three new bandicoots (Marsupialia; Peramelemorphia) from Riversleigh's Miocene deposits, north-western Queensland, Australia. *Journal of Vertebrate Paleontology 33*, 153–168.

Travouillon, K.J., Beck, R., Hand, S.J. & Archer, M., 2013b. The oldest fossil record of bandicoots (Marsupialia; Peramelemorphia) from the late Oligocene of Australia. *Palaeontologia Electronica 16*, 13A.

Travouillon, K.J., Hand, S.J., Archer, M. & Black, K., 2014a. Earliest modern bandicoot and bilby (Marsupialia, Peramelidae and Thylacomyidae) from the Miocene of the Riversleigh World Heritage Area, northwestern Queensland, Australia. *Journal of Vertebrate Paleontology 34*, 375–382.

Travouillon, K.J., Archer, M., Hand, S.J. & Muirhead, J., 2014b. Sexually dimorphic bandicoots (Marsupialia: Peramelemorphia) from the Oligo-Miocene of Australia, first cranial ontogeny for fossil bandicoots and new species descriptions. *Journal of Mammalian Evolution 22*, 1–27.

Van Dyke, S. & Strahan, R., 2008. *The Mammals of Australia*. Queensland Museum, Brisbane, 887 pp.

Voss, R. & Jansa, S., 2003. Phylogenetic studies on didelphid marsupials II. Nonmolecular data and new IRBP sequences: separate and combined analyses of didelphine relationships with denser taxon sampling. *Bulletin of the American Museum of Natural History 276*, 1–82.

Waterhouse, G.R., 1838. *Catalogue of the Mammalia Preserved in the Museum of the Zoological Society* (second edition). Richard and John E. Taylor, London, 68 pp.

Westerman, M., Kear, B., Aplin, K., Meredith, R., Emerling, C. & Springer, M., 2012. Phylogenetic relationships of living and recently extinct bandicoots based on nuclear and mitochondrial DNA sequences. *Molecular Phylogenetics and Evolution 62*, 97–108.

Woodburne, M., MacFadden, B., Case, J., Springer, M., Pledge, N., Power, J., Woodburne, J. & Springer, K., 1993. Land mammal biostratigraphy and magnetostratigraphy of the Etadunna Formation (Late Oligocene) of South Australia. *Journal of Vertebrate Paleontology 13*, 483–515.

Woodhead, J., Hand, S.J., Archer, M., Graham, I., Sniderman, K., Arena, D.A., Black, K.H., Godthelp, H., Creaser, P., Price, E., in press. Developing a radiometrically-dated chronologic sequence for Neogene biotic change in Australia, from the Riversleigh World Heritage Area of Queensland. *Gondwana Research*.

Wroe, S., 1999. The geologically oldest dasyurid, from the Miocene of Riversleigh, north-west Queensland. *Paleontology 42*, 501–527.